Rapid zoobenthic community responses to accumulations of drifting algae

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ABSTRACT: In the northern Baltic Sea, occurrences of benthic drifting macroalgal mats have become an increasing problem. Accumulations of algae induce hypoxia and anoxia in zoobenthos above the halocline on shallow sandy bottoms. The immediate and temporal responses of a macrozoobenthic community to accumulations of drifting algal mats were studied in a field experiment on an exposed shallow sandy bottom (7.5 m depth) in the northern Baltic Sea. Experimental algal plots (50 × 50 cm) corresponding to amounts recorded in the field (440 g dwt m⁻²) were enclosed in net-bags and attached to the bottom. Changes in zoobenthic community structure under the algae were compared with ambient control plots for a period of 5 wk with sampling every seventh day. Community parameters (species, abundance and biomass) in the control community remained stable. Structural differences were recorded after 9 d, and community breakdown after 16 to 21 d of algal cover. Only opportunists and species tolerant to hypoxia remained under the algae. High particulate organic C/N ratios in the sediment under algal plots were recorded after 4 wk, indicating deposition of organic material from the algae to the sediment. Initial recovery (5 d) after terminated algal stress was rapid and dominated by a mass invasion of hydrobiid snails, possibly attracted by enrichment of the sediment. Laboratory tests on algal degradation showed a 10-fold increase in phosphorus in the water due to nutrient leakage during hypoxia (20% O₂). Algal cover, and the induction of hypoxia through degradation of the algae, exhibited severe effects on zoobenthic community structure and a potential to accelerate local eutrophication. We therefore feel that the escalating amounts of drifting algae recorded in the field are a significant threat to the coastal biota.

KEY WORDS: Drifting algae · Zoobenthos · Hypoxia · Community structure · Recovery · Baltic Sea

INTRODUCTION

During recent years, occurrences of drifting algal mats have increased in shallow coastal areas all around the Baltic Sea. Both field and experimental studies have demonstrated the negative effects on the benthos (Ólafsson 1988, Bonsdorff 1992, Norkko & Bonsdorff 1996). The role of subtidally occurring algae is increasing and they pose a significant threat to the coastal biota by altering habitat characteristics and disturbing community interactions.

In ecological theory, the concept of disturbance and its role in structuring populations and communities has been given considerable attention (Pickett & White 1985, Pickett et al. 1989, Lake 1990). Pickett & White (1985) defined disturbance as a biological, chemical, or

physical event which alters or destroys the physical environment or available resources such as food and space. Disturbance might influence the structure and function of animal assemblages by directly or indirectly killing, displacing, or damaging components of the community. The effects are dependent of the frequency and intensity of the disturbance, whereas the responses depend on the inherent resilience and stability of the community. The 'intermediate disturbance hypothesis' (Connell 1978) suggests that the highest diversity in communities is found where disturbance occurs at intermediate frequencies and intensities. Frequently occurring disturbances may disrupt interactions between species and the availability of resources, producing a mosaic of patches in different sequences of a successional pattern, thus contributing to community heterogeneity (e.g. Connell 1978, Thistle 1981, Sousa 1984, Connell & Keough 1985, Pickett & White 1985).

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Seasonally occurring benthic macroalgal mats are a prominent feature in coastal areas around the world and the algae have been recognized as structuring zoobenthic communities. On tidal flats, algae such as *Ulva*, *Enteromorpha* and *Cladophora* spp. grow attached to the intertidal soft bottoms, although loose-lying forms also occur (Perkins & Abbott 1972, Nicholls et al. 1981, Soulsby et al. 1982, Reise 1983, Hull 1987, Raffaelli et al. 1991, Isaksson & Pihl 1992, Thybo-Christesen et al. 1993). Along rocky coasts, the benthic algal mats are derived from the littoral after being fragmented, detached and transported to the sublittoral, where they form loose-lying drift algal mats (e.g. Rosenberg 1985, Thrush 1986, Ólafsson 1988, Bonsdorff 1992). The coastal waters of the semi-enclosed brackish Baltic Sea have been shown to be susceptible to anthropogenic inputs (Nehring & Matthäus 1991, Gray 1992) and hence the increasing eutrophication of the Baltic has become evident at most levels of the biota through increased production above the halocline (Cederwall & Elmgren 1980, 1990, HELCOM 1990, Bonsdorff et al. 1991, Nehring & Matthäus 1991, Jumppanen & Mattila 1994). The archipelago waters of the northern Baltic Sea are characterized by a vast mosaic of islands and skerries with a long shoreline in relation to surface area (Bonsdorff & Blomqvist 1993) and an average depth of only 20 to 25 m. One obvious effect of eutrophication is the increased production of opportunistic filamentous algae which are capable of rapidly exploiting elevated amounts of nutrients (Wallentinus 1984, Kautsky 1991). A significant increase in the production of filamentous green and brown algae has been recorded in the Archipelago Sea of southwest Finland (Mäkinen & Aulio 1986, Jumppanen & Mattila 1994). Mechanical loss of algal material results in the transportation of algae to the benthic systems and hence the increased production is reflected as increasing amounts of organic material in the form of drifting algae (Bonsdorff 1992, Bonsdorff et al. 1995, Norkko & Bonsdorff 1996). These mats frequently occur on shallow sandy bottoms above 15 m depth with patches ranging in size from a few m² to hectare size and modify normally uncovered areas with both promotive and repressive influences on the benthic community (Norkko & Bonsdorff 1996). Due to the elevated amounts and frequencies of occurrence, they pose a growing threat to shallow benthic communities. Drifting algae act as a physical as well as a biological factor, with the reduction of water exchange and with algal decay inducing hypoxia and anoxia in the interstitial (Reise 1983, Hull 1987), as well as the water at the algal-sediment interface (Norkko & Bonsdorff 1996). The response of the infaunal community to the unfavourable conditions is dependent of species-specific tolerance, mobility and

size on the algal mat. We have shown earlier that short-term exposure (hours to days) at high temperatures induces an escape reaction in the infauna, enhancing prey availability (Norkko & Bonsdorff 1996). The effects of algal mats are further pronounced since their maximum occurrence coincides with the most productive period of the year, in July and August (Bonsdorff 1992, Bonsdorff et al. 1995, Norkko & Bonsdorff 1996). Algal mats have been acknowledged as a factor inducing widespread mortality in benthic infauna (Perkins & Abbott 1972, Soulsby et al. 1978, 1982, Williams Cowper 1978, Nicholls et al. 1981, Thrush 1986, Hull 1987, Everett 1991, Raffaelli et al. 1991, Bonsdorff 1992, Peterson et al. 1994). Very little, however, is known about the actual mechanisms causing the impoverishment on a temporal scale. Although Thrush (1986) conducted an experiment with decaying laminarian seaweeds, illustrating the structuring potential of the algae on zoobenthos over time, most of the literature regards attached algae on tidal flats (Hull 1987, Raffaelli et al. 1991). Loose-lying drifting algal mats are expected to affect zoobenthic communities in a more haphazard manner due to their unpredictable occurrences. The effects of the disturbance are dependent on the temporal and spatial scale of the occurrences of drifting algal mats, i.e. the frequency, constancy and amplitude of disturbance. It is therefore essential to assess the temporal response of zoobenthic communities to accumulations of drift algae in order to be able to correctly interpret their role as structuring factors on coastal zoobenthos.

We report results here from a field experiment of drifting algal mats and their importance as structuring factors on a zoobenthic community. The response of the zoobenthic community, with emphasis on the immediate temporal response to the continuous stress by drifting algal mats, was assessed in a controlled field manipulation experiment with artificially enhanced algal cover.

MATERIAL AND METHODS

Study site. The field experiment was conducted in the outermost Åland archipelago in the central northern Baltic Sea (60° 17' N, 19° 49' E). The locality, covering an area of approximately 6 ha, is a semi-exposed sound between 2 islets and is exposed to the northwest. The depth ranges from 5 to 10 m and the sediment consists of medium to fine sand (median grain sizes 0.125 to 0.250 mm; loss on ignition ~0.45%). During summer (May to August), temperature ranges from about 6 to 17°C and salinity varies between 5.9 and 6.2‰. Oxygen saturation in the bottom water is usually high (>100%), although local oxygen deficiency and

anoxia has been recorded in connection with accumulations of drifting algal mats (Bonsdorff 1992). Dominating macrofauna are *Macoma balthica* (L.), gastropods (*Hydrobia* spp.), polychaetes [*Pygospio elegans* Claparède, *Manayunkia aestuarina* (Bourne), *Nereis diversicolor* (O. F. Müller)] and oligochaetes. The main invertebrate predators in the area are *Saduria entomon* (L.) and *Crangon crangon* (L.), whereas the most important benthivorous fish are flounder *Platichthys flesus* (L.) and gobies (Norkko 1993, Bonsdorff et al. 1995). The littoral vegetation is dominated by *Cladophora glomerata*, *Enteromorpha intestinalis*, *Pilayella littoralis* and *Fucus vesiculosus* (Haldin 1994). Since the beginning of the 1990s, the production of opportunistic macroalgae has increased, as has the subsequent occurrences of drifting algal mats from 150 to an average of 450 g dwt m⁻², and maximum biomasses of 880 g dwt m⁻² have been recorded (Bonsdorff 1992).

During a 6 wk period (July through mid-August) in 1993, a drift algal mat covered 2 ha of the bottom. The biomass was estimated at 440 ± 16 g dwt m⁻². The algal mat showed signs of increasing deterioration with the development of bacterial mats (*Beggiatoa* spp.) on the algae. Locally the conditions under the mat were anoxic with hydrogen sulphide present.

Experimental set-up and sampling. The accumulations of drifting macroalgal mats and their impact on the zoobenthic community were studied at a depth of 7.5 m during 34 d (from August 11 to September 14, 1993). The locality chosen represented a homogenous area which had not been subjected to long-term exposure by drifting algal mats, although some short-term exposure could not be ruled out due to the unpredictable movements of the algal mat. Species composition, life-strategy and relative biomasses of the drift algal species are accounted for in Table 1 (nomenclature according to South & Tittley 1986). Algae were collected with an Ockelmann-sledge and were carefully rinsed with seawater in the laboratory to remove macrofauna. Quantitative algal samples for the determination of biomass were taken according to Bonsdorff (1992). An amount of ~510 g ww (2050 g ww m⁻² = 440 g dwt m⁻²) was sewn into 30 net-bags measuring 50 × 50 cm (mesh size: 1.5 cm). The net-bags were placed on the bottom and anchored with wire in 2 rows 50 cm apart covering an area of 22.5 m⁻². The design was chosen in order to facilitate sampling

Fig. 1 Experimental design of the field experiment. Graph illustrates the treatments, their durations, and the sampling sequences. Ref. sand: reference, sand; Ref. algae: reference, algae; C1–6: controls; A1–5: algae; Rec1–4: recovery; *reference samples (n = 5) from bare sand and under naturally drifting algal mats on Day 0

by SCUBA diving. The net-bags were loose enough for the algae to form a naturally behaving algal mat. During the experiment, the benthic community was sampled under the algae by removing the net-bags over time (on 5 occasions) and comparing the response with ambient control situations (6 occasions, Fig. 1). On each occasion, 6 replicate net-bags with algae were randomly removed and macrofauna was sampled in

Table 1 Species composition, life strategy and relative biomasses (% share) of the different species comprising the drifting algal mat. Life-strategy according to Wallentinus (1984). A: annual; P: perennial; +: fragments

Division	Species	Life-strategy	Biomass (g dwt)
Rhodophyta	<i>Ceramium tenuicorne</i> Waern	A	1.8%
	<i>Rhodomela confervoides</i> (Huds.) Silva	P	
	<i>Polysiphonia nigrescens</i> (Huds.) Grev.	P	
Phaeophyta	<i>Fucus vesiculosus</i> L.	P	2.9%
	<i>Chorda filum</i> (L.) Stackh.	A	
	<i>Stictyosiphon tortilis</i> (Rupr.) Reinke	A	27.6%
	<i>Dictyosiphon foeniclaceus</i> (Hudson) Grev.	A	
	<i>Pilayella littoralis</i> (L.) Kjellmann	A	63.1%
	<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngb	A	
	<i>Furcellaria lumbricalis</i> (Huds.) Lamouroux	P	4.3%
Chlorophyta	<i>Cladophora rupestris</i> (L.) Kuetz.	P	0.9%
	<i>Monostroma balticum</i> (Aresch.) Wittr.	A	
	<i>Cladophora glomerata</i> (L.) Kuetz.	A	
(Charophyta)	<i>Tolypella nidifica</i> (O. Müll.) Leonh.	-	+
Magnoliophyta	<i>Ruppia spiralis</i> L.	-	+
	<i>Zostera marina</i> L.	-	+

the center of the underlying sediment surface; similarly, 6 replicate control samples were randomly taken from the ambient area, using a benthic core-sampler (4.7 cm diameter, 10 cm into the sediment). Further, 3 smaller core-samples (2.5 cm diameter, 5 cm into the sediment) for the determination of loss on ignition and the analyses of particulate organic carbon (POC) and particulate organic nitrogen (PON) in the sediment were taken under the algae and control conditions, respectively. On every occasion, algae were collected for the measurements of POC and PON from 3 of the net-bags. After the removal of algae and the benthic samples, the plots were marked with iron rods and revisited after 5 d to take samples for initial faunal recovery rates. Samples for loss on ignition were determined according to Dybern et al. (1976). All macrofauna samples were fixed in 4% buffered formalin. After washing on a 0.5 mm mesh sieve, the remaining animals were removed, counted and identified to species/taxa under a preparation microscope (15× magnification). The sediment and algae were analyzed for POC and PON content after drying and homogenizing the samples. The measurements were done using a LECO[®] CHN-900 element analyser. At the start and at the end of the experiment, water samples for the analysis of chlorophyll *a* were taken from the bottom water. Before the ending of each algal treatment (removal of algae), water samples were taken with a syringe underneath the algae for measurements of temperature and oxygen concentration.

The experiment consisted of 15 treatments: 6 control treatments (C1, C2, C3, C4, C5 and C6), 5 treatments with algae (A1, A2, A3, A4 and A5) and 4 recovery treatments (Rec 1, 2, 3 and 4; Fig. 1). In addition to these treatments, macrofauna samples were taken under naturally occurring drifting algal mats (Ref. algae) and from a nearby uncovered bottom area (Ref. sand) at Day 0 (start of the experiment). The experimental set-up and sampling sequences of macrofauna are presented in Fig. 1.

Laboratory experiment. A small-scale experiment was conducted in the laboratory in order to study the possible hypoxic conditions induced by algae and subsequent leakage of nutrients during decomposition. The experiment consisted of 2 treatments: control (no algae), and algae. In both treatments, 1 aquarium (25 × 35 × 40 cm) with a 6 cm layer of sieved and air-dried sediment was used. To the algal treatment, 175 g ww (2000 g ww m⁻²) loose-lying algae was added on top of the sediment. Both aquaria were oxygenated with aquarium air pumps. A perforated tube was placed under the algae at the start of the experiment in order to obtain samples for the analyses of temperature and oxygen concentration. Temperature and oxygen levels were measured with a portable DO-meter (calibrated

with Winkler titration) at least twice daily in both treatments. The experiment lasted 17 d, and ended when the degradation process in the algae resulted in rapid discolouration of the water and a strong smell of hydrogen sulfide. At the end, water samples for organic and inorganic fractions of nitrogen and total phosphorus were taken from both treatments. All chemical analyses were performed according to Grasshoff et al. (1983).

Data analysis. For the analysis of the community patterns, a cluster analysis was performed for detecting natural groupings in the data (using SYSTAT 5.0[®]). A dendrogram was constructed based on a Euclidean distance matrix and the average-linkage (UPMGA) clustering method. The clustering was performed using the abundance values of the 7 most dominant species/taxa of the community which were constantly present in either control or algal treatments. For each replicate sample in all treatments the Shannon-Wiener diversity index (*H'*) and its evenness component (*J*) was calculated. Analysis of the macrofaunal data revealed non-normality of distribution (Shapiro-Wilk *W*-test) and heterogeneity of variances (Bartlett's test). The statistical analysis was therefore performed using the non-parametric Kruskal-Wallis *H*-test (Sokal & Rohlf 1981). In order to test for the differences between treatments, pairwise comparisons of the mean ranks were made using the formula described in Sachs (1982) which corrects for unequal sample size. Where possible, Student *t*-test and ANOVA were used. When comparing recovery after algal stress (algal treatment → recovery treatment), the non-parametric Wilcoxon signed-rank test for dependent samples was performed. All data are presented as mean values ± standard error ($\bar{x} \pm \text{SE}$) m⁻².

RESULTS

Nutrient leakage from macroalgae

The hydrographical conditions were stable throughout the experiment (Table 2). Average temperature in the control treatment was $9.6 \pm 2.1^\circ\text{C}$ and oxygen saturation $98 \pm 1\%$. The temperature under algae was significantly higher (pooled data of 17 d; $p < 0.001$, Student *t*-test) than in the water above the algae. Within 24 h, the oxygen saturation declined to below 20% oxygen saturation and was stable over time with an average of $21 \pm 2\%$ oxygen saturation under algae (Table 2). The hypoxic conditions under the algae gave a 10-fold elevation of total phosphorus in the water compared to control (total-P = 1.0 mg l^{-1} under algae vs 0.09 mg l^{-1} in control), indicating a release from the decomposing algae under hypoxia. In the algal treatment the inorganic nitrogen fractions (NH_4^+ , NO_2^- and

Table 2. Hydrographic and physico/chemical conditions in the aquaria from the laboratory experiment on the degradation of an algal mat. Control: no algae; Algae: algal biomass corresponding to 2000 g ww_t m⁻²; Under/Over: conditions under and over the algal mat

Conditions	Control	Algae	
		Under	Over
Temperature			
$\bar{x}$ °C ± SE	9.6 ± 2.1	9.8 ± 2.1	9.5 ± 2.3
Min.–max. °C	7.2–11.8	6.7–11.9	6.4–11.6
Oxygen			
$\bar{x}$ % ± SE	98 ± 1	21 ± 2	92 ± 1
Min.–max. %	96–109	1–99	73–99
Total P (mg l ⁻¹)	0.09	1.0	0.54
Total N (mg l ⁻¹)	1.5	2.9	1.8
NH ₄	0.11	0	0
NO ₂	0.02	0	0
NO ₃	0.66	0.04	0.03
Total organic N	0.71	2.9	1.8

NO₃⁻) were lower than in the control, indicating a shift from denitrification to the reduction of sulfate (S₂⁻). This is confirmed by the presence of H₂S (strong smell) (Table 2). Further, heterotrophic bacteria such

as *Beggiatoa* spp. which occur at the interface between the anoxic sulfide-liberating zone and the overlying oxic zone are known to utilize ammonia (NH₄⁺) and nitrite (NO₂⁻) (Strohl 1989). The large fraction of organically bound nitrogen (99% of the total nitrogen pool) could reflect high biomasses of bacteria (Table 2).

Observations from the study site

The algae enclosed in net-bags were rapidly colonized by a large number of grazing and predatory invertebrates. The most dominant faunal components were gastropods (*Hydrobia* spp.), gammarid amphipods, the isopods *Idothea balthica* and *Saduria entomon*, the nemertean *Prostoma obscurum*, the polychaete *Nereis diversicolor* and turbellarians (Table 3). After 9 d (A2, Fig. 1), the sediment surface under the algal treatments was completely black, adult *Macoma balthica* were noted on the sediment surface and some clams had migrated into the algae. The same phenomena with clams on the sediment surface and the appearance of a black sediment surface were observed under natural accumulations of

Table 3. List of species/taxa found in the set of treatments (Control, Under algae, Recovery). +: Species found; -: not found; •: pooled occurrences from the last 2 sampling occasions in control (C5 and C6) and under algae (A4 and A5). Last column (In algae) indicates the species recorded in algal mats and is based on qualitative data from the experiment and field surveys

Family	Species/taxa	Control	Under algae	Recovery	In algae
Mollusca	<i>Theodoxus fluviatilis</i> (L.)	+	+	-	+
	<i>Lymnea peregra</i> (Müller)	-	-	-	+
	<i>Hydrobia ventrosa</i> (Montagu)	•	•	+	+
	<i>Hydrobia ulvae</i> (Pennant)	•	+	+	+
	<i>Mytilus edulis</i> L.	+	+	+	+
	<i>Cerastoderma glaucum</i> (Bruguire)	•	+	-	+
	<i>Macoma balthica</i> (L.)	•	•	+	+
	<i>Embletonia pallida</i> Alder + Hancock	-	-	-	+
	<i>Saduria entomon</i> (L.)	-	-	+	+
Crustacea	<i>Idothea baltica</i> Pallas	-	-	-	+
	<i>Jaera albifrons</i> Leach (coll.)	-	-	-	+
	<i>Corophium volutator</i> (Pallas)	•	-	-	+
	<i>Gammarus oceanicus</i> Segerstråle	-	-	-	+
	<i>Gammarus</i> spp.	-	+	+	+
	<i>Crangon crangon</i> (L.)	•	-	-	+
	Ostracoda	•	+	+	-
	<i>Nereis diversicolor</i> O.F. Müller	•	•	+	+
Polychaeta	<i>Harmothoe sarsi</i> (Kinberg)	+	-	-	+
	<i>Pygospio elegans</i> Claparede	•	+	+	-
	<i>Manayunkia aestuarina</i> (Bourne)	•	•	+	-
Hirudinea	<i>Piscicola geometra</i> (L.)	-	-	-	+
Oligochaeta		•	•	+	+
Nemertina	<i>Prostoma obscurum</i> Schultze	•	+	+	+
Turbellaria	<i>Dendrocoelum lacteum</i> (O.F. Müller)	-	-	-	+
	<i>Planaria torva</i> O.F. Müller	-	-	-	+
Insecta	Chironomidae	+	-	+	+
Pisces	<i>Zoarces viviparus</i> (L.)	-	-	-	+
	<i>Pomatoschistus minutus</i> (Pallas)	+	-	-	+
	<i>Pungitius pungitius</i> (L.)	-	-	-	+

algae. After 16 d (A3), the algae in the net-bags showed clear signs of deterioration with a gradual formation of mats of sulphur bacteria (*Beggiatoa* spp.). Towards the end of the experiment (A5, 29 d), all algal net-bags were completely covered with bacteria. When removing algae during the experiment, epibenthic predators such as gobiids and brown shrimps *Crangon crangon* were observed to rapidly accumulate around/on the exposed plots, possibly exploiting stressed infauna at the sediment surface. At the end of the experiment, adult *N. diversicolor* were observed (individuals and characteristic burrows) under the algal treatments A4 and A5. *N. diversicolor* is known to be tolerant to hydrogen sulfide (Vismann 1990) and to function as an infaunal predator (Rönn et al. 1988).

Hydrographical conditions during the experiment

At the end of August and beginning of September, water temperatures decrease rapidly in the archipelago waters, and during the experiment average temperature in the bottom water declined from ~16 to 11°C. The chlorophyll *a* of the bottom water declined from 12 $\mu\text{g l}^{-1}$ at the start of the experiment to 1.6 $\mu\text{g l}^{-1}$ towards the end of the experiment. At the end of the experiment, slightly higher temperatures were recorded under the algal plots (13°C) compared to the free bottom water (11.5°C, Fig. 2a). Oxygen content decreased to moderately hypoxic conditions under the algal plots after only 9 d of exposure (Fig. 2b).

POC/PON and loss on ignition

The POC values of the algae showed a significant ($p < 0.05$) initial decline from $180 \pm 17 \text{ mg g}^{-1} \text{ dwt}$ to levels around $125 \text{ mg POC g}^{-1} \text{ dwt}$, thereafter remaining constant over time. The same significant decline was recorded for PON. Despite a steady decline over time, there was no significant change in the POC/PON ratio of the algae. In the control treatments (bare sand) and the treatments under algae, the only significant changes were recorded under algae in treatment A5 (the last treatment before termination of the experiment). This treatment had significantly higher ($p < 0.05$) POC values ($18 \pm 8 \text{ mg g}^{-1} \text{ dwt}$) and POC/PON ratios (C/N ratio 19 ± 6) than all other treatments of both control and under algae (Fig. 3). No changes in loss on ignition between control and algal treatments were recorded during the course of the experiment, with values ranging between 0.41 and 0.53 %.

Fig. 2. Hydrographical conditions during the experiment in the free bottom-water (control) and under algae. (a) Temperature (°C), and (b) oxygen concentration (mg l^{-1})

Fig. 3. Changes in (a) POC/PON ratios and (b) the fraction of POC in bare sand (control), under the algal plots and in the algae over the experimental time. Note that in (b) POC values for algae are divided by 10

Community structure under natural occurrences of algae

The zoobenthic community sampled under naturally occurring algae had been exposed to drifting algal mats for approximately 1 mo. Community parameters exhibited significant reductions ($p < 0.001$) compared to controls (Fig. 4, Tables 4 & 5). The average number of species found was 5.3 ± 0.2 on bare sand (Ref. sand, Fig. 1) compared to 2.0 ± 0.6 under algae (Ref. algae,

Fig. 1), with oligochaetes as the dominant faunal component. Abundance values were reduced by 87% under the algae from (24.2 ± 5.2) to $(3.1 \pm 1.6) \times 10^3$ ind. m^{-2} . Biomass was reduced by 94% from 107 ± 23 to 7 ± 3 g wwt m^{-2} (Fig. 4). Diversity (H') was also found to be reduced from 1.54 ± 0.17 to 1.11 ± 0.2 . Evenness (J) showed higher values in Ref. algae (0.79 ± 0.08) compared to Ref. sand (0.63 ± 0.07), however, illustrating the dominance by oligochaetes.

Table 4. Statistical differences (Kruskal-Wallis; pair-wise comparisons) between no. of species (left side of table) and biomass (right side of table) for the different treatments. Levels of significance are given for all combinations of treatments tested. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns: is not significant

Levels of significance for species	Treatments	Days	Levels of significance for biomass																
			Ref. s	Ref. a	C1	A1	C2	A2	Rec 1	C3	A3	Rec 2	C4	A4	Rec 3	C5	A5	Rec 4	C6
	Ref. sand	0		***	ns	ns	ns	***	***	ns	***	ns	ns	***	*	*	***	ns	ns
	Ref. algae	0	***		***	***	***	***	***	***	***	***	***	ns	***	***	***	***	***
	Control 1	3	ns	***		***	ns	***	***	ns	**	ns	**	***	ns	ns	ns	ns	**
	Algae 1	3	**	***	***		ns	ns	ns	*	***	*	ns	***	***	***	***	***	ns
	Control 2	9	ns	***	ns	ns		***	***	ns	***	ns	ns	***	ns	ns	***	***	ns
	Algae 2	9	ns	***	ns	ns	ns		ns	***	***	***	*	***	***	***	***	ns	ns
	Rec 1	14	ns	***	ns	ns	ns	ns		***	***	***	ns	***	***	***	***	ns	ns
	Control 3	14	ns	***	ns	***	ns	ns	ns		***	ns	ns	***	ns	ns	*	***	ns
Algae 3	16	***	***	***	ns	***	***	***	***		ns	***	ns	ns	ns	ns	***	***	
Rec 2	21	***	***	***	ns	***	***	***	***	ns		ns	***	ns	ns	ns	***	ns	
Control 4	21	ns	***	ns	***	ns	ns	*	ns	***	***		***	***	***	***	ns	ns	
Algae 4	23	***	ns	***	***	***	***	***	***	***	***	***		ns	***	***	***	***	
Rec 3	28	***	***	***	ns	***	***	***	***	ns	ns	***	ns		ns	ns	***	***	
Control 5	28	ns	***	ns	***	ns	ns	ns	ns	***	***	ns	***	***		ns	***	***	
Algae 5	29	***	ns	***	***	***	***	***	***	***	***	***	ns	***	***	*		***	
Rec 1	34	ns	***	*	ns	ns	ns	***	***	ns	ns	***	***	*	***	ns		ns	
Control 6	34	***	***	**	***	***	***	***	*	***	***	ns	***	***	ns	***	***		

Table 5. Statistical differences (Kruskal-Wallis; pair-wise comparisons and Wilcoxon signed-rank) between abundance in the different treatments (left side of diagram). Right side of diagram illustrates the normalized Euclidean distances between every pair of variables, based on the abundance of the 7 most dominant species. Levels of significance are given for all combinations of treatments tested. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns: not significant

Treatments	Days	Euclidean distances for abundance																	
		Ref. s	Ref. a	C1	A1	C2	A2	Rec 1	C3	A3	Rec 2	C4	A4	Rec 3	C5	A5	Rec 4	C6	
Levels of significance for abundance	Ref. sand	0		60	23	40	39	19	481	14	56	145	34	59	72	30	61	72	32
	Ref. algae	0	***		38	24	98	47	540	74	13	204	92	4	131	88	6	127	90
	Control 1	3	ns	***		18	60	14	503	37	36	167	55	37	94	50	39	93	53
	Algae 1	3	***	***	ns		77	25	519	54	28	183	71	23	109	66	24	111	69
	Control 2	9	***	***	***			54	444	26	94	108	13	98	38	14	99	46	11
	Algae 2	9	ns	***	ns	ns	***		494	32	48	158	47	46	85	42	47	91	45
	Rec 1	14	***	***	***	***	***	*		467	537	337	448	540	410	453	541	423	451
	Control 3	14	ns	***	***	***	ns	***	***		70	131	21	73	59	19	75	59	20
	Algae 3	16	***	*	ns	ns	***	ns	***	***		201	90	16	128	85	18	120	88
	Rec 2	21	***	***	***	***	ns	***	ns	***	*		112	203	51	117	204	95	115
	Control 4	21	ns	***	***	***	ns	***	***	ns	***	ns		91	39	8	93	53	7
	Algae 4	23	***	ns	***	***	***	***	***	***	ns	***	***		130	87	2	128	90
	Rec 3	28	***	***	***	***	ns	***	***	ns	***	ns	ns	*		45	131	51	42
	Control 5	28	ns	***	*	***	*	*	***	ns	***	***	ns	***	*		88	58	5
Algae 5	29	***	ns	***	*	***	***	***	***	ns	***	***	ns	***	***		129	91	
Rec 1	34	***	***	***	***	ns	***	ns	***	***	ns	***	***	ns	***	*		55	
Control 6	34	***	***	***	***	ns	***	***	ns	***	ns	ns	***	ns	ns	***	**

Fig. 4. (a) Species, (b) abundance and (c) biomass of the zoobenthic community exposed to natural accumulations of drifting algal mats over a period of 1 mo

Changes in species, abundance and biomass under algal plots

The zoobenthic community consisted of 17 invertebrate species/taxa (Table 3). The 7 most dominant species were *Macoma balthica*, *Hydrobia* sp., *Pygospio elegans*, *Manayunkia aestuarina*, *Nereis diversicolor*, *Prostoma obscurum* and oligochaetes. A regression analysis revealed that mudsnails explained 91% of the total variation in abundance, whereas *M. balthica* explained 96% of the variation of total biomass in the data-set. The Kruskal-Wallis *H*-test gave significant differences in species numbers ($H = 55.2$, $df = 16$, $p < 0.0001$). C6 (Fig. 1) differed significantly from all other control treatments, illustrating the gradual increase in species number over time (6.7 ± 0.5 species in C6 compared to 5.5 ± 0.5 in C1; Fig. 5a). Despite a slight (non-significant) initial increase in species numbers under algae, from 4.5 ± 0.3 species in A1 to 5.2 ± 0.6 species in A2, the number of species showed a significant

decline after 16 d (A3) compared to control treatments and A2. Toward the end of the experiment, only 1.8 ± 0.5 and 2.2 ± 0.5 species were left in A4 and A5 respectively (Fig. 5a, Table 4).

Significant differences were also recorded in abundance ($H = 78.0$, $df = 16$, $p < 0.0001$). After an initial overshoot after 9 d (C2, Fig. 1), the abundance values were relatively constant at levels of around 30×10^3 ind. m⁻² in the control treatments (Fig. 5b). There was a significant decline under algae (A2 vs C2) after 9 d of algal stress (Fig. 5b, Table 5). A rapid decline in abundance followed with a breakdown in A4 and A5, with an approximately 90% reduction compared to the control treatments C5 and C6. At the end of the experiment (A5), only $(3.2 \pm 1.2) \times 10^3$ ind. m⁻² remained under algae compared to $(33.2 \pm 2.9) \times 10^3$ ind. m⁻² in C6 (Fig. 5b, Table 5).

Fig. 5. Comparison of (a) species, (b) abundance and (c) biomass under algae (440 g dw m^{-2}) and control (no algal cover). Note the reference treatments (Ref. sand and Ref. algae)

Biomass values were less consistent than the species and abundance patterns, probably due to the great inherent variability in the adult fraction of the *Macoma balthica* population ranging between 98 and 188 g wwt m⁻² in control treatments and 19 and 393 g wwt m⁻² in the algal treatments (Kruskal-Wallis; $H = 38.4$, $df = 16$, $p < 0.0013$). C4 and C6 had significantly higher biomass than C1 and C5 (Fig. 5c, Table 4). The biomass under algae showed a significant increase after 9 d (Fig. 5c, Table 4), increasing from 209 ± 73 g wwt m⁻² in A1 to 393 ± 145 g wwt m⁻² in A2. A2 differed significantly from all other treatments except A1 and C6 (Table 4). This is probably partly explained by adult *M. balthica* emerging closer to the sediment surface under the influence of algal cover, and partly by the stochastic occurrence of gastropods such as *Theodoxus fluviatilis* in the samples. Toward the end of the experiment (A4 and A5), biomass was significantly reduced (19 ± 14 and 55 ± 24 g wwt m⁻², respectively) compared to control treatments C5 and C6.

Changes in community diversity under algal plots

The initial diversity in the control treatment (C1, Fig. 1) was 1.82 ± 0.07 and was significantly ($p < 0.05$) reduced in the other, subsequent control treatments

(C2 to C6, Fig. 6a). Algal treatment A1 had a high diversity value (1.71) which then gradually declined (A2 = 1.62 to A5 = 0.96). After 9 d (A2), this decline was significant ($p < 0.001$) compared to A1, stabilizing at low levels towards A4 and A5 (0.94 and 0.96, respectively). A4 and A5 differed significantly ($p < 0.05$) from C4, C5 and C6, illustrating community breakdown under algae (Fig. 6a).

Higher values of evenness were found under algae compared to the control treatments, throughout the experiment. In the control treatments the initially high values declined from 0.74 ± 0.07 in C1 to 0.56 ± 0.07 in C6, illustrating the gradual recovery from stress imposed by the natural drifting mats which probably had occurred in the area at the start of the experiment (Fig. 6b). Despite an initial decrease in evenness under algae at the start of the experiment, the evenness values rose towards the end (A4 = 0.81 ± 0.08 , and A5 = 0.80 ± 0.07), illustrating the gradual takeover of community dominance by species indifferent to algal stress (mainly oligochaete species) (Fig. 6b). The differences between control and algal treatments were already significant ($p < 0.05$) after 9 d (C2 vs A2, Fig. 1).

Short-term recovery after algal stress

Recovery samples were taken 5 d after the algal net-bags had been removed, from treatment A2 onward. As the recovery samples were directly linked to the conditions after algal stress the Wilcoxon signed-rank test was performed and statistical power (df) was lost compared to the Kruskal-Wallis H -test (1 vs 16 df). For numbers of species, there was no significant difference in recovery from algal stress throughout the experiment (Fig. 7a, Table 4) and the 5 d recovery treatments failed to reach control levels. Although not significant, the recovery rates increased over time (Fig. 7a, Table 4).

The impoverishment after algal stress was followed by overshoots in abundance in the recovery treatments (Fig. 7b) compared to both algal and control treatments. The recovery process was completely dominated by mudsnails (*Hydrobia* sp.). Recovery from the algal treatments A2 to A5 was significant ($p < 0.05$; Fig. 7b, Table 5). Rec1 exceeded abundance values of A2 by 69% and C3 by 53% ($p < 0.001$). Rec2 exceeded A3 by 83% and C4 by 47% ($p < 0.001$). Rec3 exceeded A4 by 89% ($p < 0.05$) and C5 by 14% (ns). Rec4 exceeded abundance values of A5 by 93% and C6 by 30% ($p < 0.01$; Fig. 7b, Table 5).

Biomass recovery was less consistent compared to recovery patterns in species and abundance. A non-significant decrease was found between A2 and Rec1

Fig. 6. Comparison of (a) diversity and (b) evenness under algae and control over the experimental time. Note the reference treatments (Ref. sand and Ref. algae)

Fig. 7. Immediate recolonization rates for (a) species, (b) abundance and (c) biomass during a 5 d period after the removal of algal cover. Arrows indicate recolonization after stress. Shaded area indicates background control levels

(393 ± 145 to 221 ± 54 g wwt m^{-2}). Only Rec4 exhibited a significant ($p < 0.05$) increase compared to A5 (from 55 ± 24 to 266 ± 82 g wwt m^{-2}). Only biomass values in Rec1 exceeded the control value of C3; all other recovery treatments were non-significant compared to their respective control treatments (Fig. 7c, Table 4).

The recovery treatments after algal stress (Rec1 to Rec5) exhibited lower diversity ($H' = 0.82$ to 1.03) compared to the situation after the algal plots were removed ($H' = 1.62$ to 0.96), with only Rec2 differing significantly ($p < 0.05$) from A2 (Fig. 8a). Evenness values decreased significantly ($p < 0.05$) compared to algae (A2 to A5) and control (C2 to C5, Fig. 8b). The changes in diversity measurements (H' and J) are largely governed by the presence or absence of *Hydrobia* sp.

Fig. 8. Immediate recolonization as illustrated by changes in (a) diversity and (b) evenness during a 5 d period after the removal of algal cover. Arrows indicate recolonization after stress. Shaded area indicates background control levels

Groupings of the data by means of hierarchical clustering

The average-linkage clustering gave a dendrogram with clearly separate clusters (Fig. 9). All control treatments, initial algal treatments (A1 and A2) and the reference from bare sand (Ref. sand) formed a cluster (Cluster 1, Fig. 9), where the Euclidean distances among the treatments within the cluster ranged between 4.8 and 76.9 (Table 5). Within Cluster 1, the treatments C2, C4, C5 and C6 formed a group which possibly indicates the gradual increase of abundance in the control community. The degradation of the community under algae (algal treatments) from Day 16 onward (A3, A4 and A5), along with the situation under natural occurrences of algae (Ref. algae) produced a distinct Cluster 2 which was characterized by low internal distances, and large distances to the other clusters (Fig. 9, Table 5). The recovery treatments formed a heterogeneous group, illustrating the stochastic pattern of recovery and may only be regarded as a group in the sense that they are recovery phase samples (Fig. 9). Rec1 differed from all other treatments (distances ranging from 337 to 541; Table 5).

Fig. 9. Dendrogram based on the Euclidean distances (nearest neighbour method) between treatments illustrates changes in community composition over experimental time. 1. and 2. indicate separate clusters. A1–5: under algae; C1–6: control treatments; Rec: recovery treatments after algal stress; Ref. s: Reference, sand; Ref. a: Reference, algae

Comparison between natural algal mats and experimental algal plots

The situation under the last 2 algal treatments (A4 and A5) was similar to the situation under the natural occurrences of algal mats (Ref. algae) in all measured community parameters, illustrating the power of the experiment in mimicking natural conditions. There was no significant difference between A5 and the situation under natural algae (Ref. algae) regarding species numbers, $A5 = 2.2 \pm 0.5$ vs 2.0 ± 0.6 for Ref. algae (Fig. 5a, Table 4).

Abundance values in A5 were $(3.2 \pm 1.2) \times 10^3$ ind. m^{-2} compared to $(3.1 \pm 1.6) \times 10^3$ ind. m^{-2} under natural algae (Ref. algae) (ns; Fig. 5b, Table 5). Similarly, there were no significant differences regarding biomass when comparing A4 (19 ± 14 g wwt m^{-2}) and Ref. algae (6.9 ± 2.9 g wwt m^{-2}), although A5 had significantly higher biomass values (Fig. 5c, Table 4). The same trend was observed for community diversity with $H' = 0.96 \pm 0.17$ in A5 and 1.11 ± 0.20 in Ref. algae.

DISCUSSION

The results give conclusive evidence of the negative effects of drifting algal mats on coastal macrobenthic communities. As stated by Ólafsson (1988), drifting algal mats change in size, density and location in response to hydrodynamical conditions and the amount of drifting algae. With increasing eutrophication, increasing problems with drifting algal mats are expected. As a distur-

bance agent for the zoobenthos, drift algae have gained in importance and changed from a mere disturber and interrupter of community interactions with partly positive effects contributing to patch dynamics (i.e. intermediate disturbance through episodic occurrences), to a factor which has the potential to completely destroy the macrozoobenthic community.

Decaying algae — organic loading and leakage of nutrients

The algae are dominated by annual species (Table 1) pronouncing the annual cyclic phenomena of decaying algae. The dominants of the algal species (i.e. the *Pilayella/Ectocarpus*-complex) exhibit clear seasonal variations in production

and nutrient content with a pronounced peak in June, whereafter they are fragmented, detached and transported to the sediment communities as drift algae (Kautsky 1995). Considerable amounts of organic matter thus enter the benthic subsystems through the deposition of macroalgae from the littoral; Kautsky (1995) estimated the benthic primary production of the filamentous algae to constitute ~25% of the total coastal production (Swedish coast) on an annual basis. Similarly, Kautsky (1995) calculated that the detached filamentous algae contributed up to 50% of the annual input of POC to coastal sediment communities.

The benthic drift algal mat acts as an integrated biological entity, which depending on status of the algae might exhibit photosynthesis, decomposition, or both. The algal mats have been shown to induce hypoxia/anoxia in the underlying sediment (Nicholls et al. 1981, Sundbäck et al. 1990, Norkko & Bonsdorff 1996). This was also confirmed in the field and laboratory experiment. The measurements of oxygen under algae are somewhat uncertain and it is likely that oxygen levels were lower or even anoxic, since hydrogen sulfide odor was present in both cases. Decomposition of algal detritus is known to be mediated by bacteria and fungi (e.g. Tenore et al. 1984), and in both experiments, bacterial mats gradually developed, illustrating the ongoing decomposition of algae. The initial amount of POC in the algae was high, illustrating the considerable potential carbon source, and a significant decrease was registered. Only at the end of the experiment was a significant increase registered in the sediment under the algae, however, indicating mineralization taking

place in the algal mat itself (Sundbäck et al. 1990). The higher POC values at the end of the experiment possibly illustrate higher nutritional levels in the sediment, which might stimulate bacterial production and subsequent immigration by epibenthic deposit feeders (Tenore et al. 1984, Levinton 1985). It is evident that the deposition of macroalgae to the sediment constitutes a large food source either directly or after bacterial enrichment, as illustrated by Vetter (1995), who recorded extremely high levels of benthic secondary production in connection to macroalgal debris in submarine canyons off the Californian coast (USA). This is also confirmed in the Baltic Sea, where the major pigment in guts of benthic fauna at the end of June to July originates from macroalgae (Kautsky 1995). Algal mats change nutrient fluxes from the sediment (Zimmerman & Montgomery 1984, Sundbäck et al. 1990). These fluxes have been shown to exhibit significant diel variation, whereas the respiration of the algae and sediment may cause oxygen deficiency (Thybo-Christesen et al. 1993). Higher temperatures were recorded under the algal mats which may further accelerate the decomposition process and the development of oxygen deficiency. Salinity stratification could cause such differences in temperature. Another explanation is that the algal mat affects hydrodynamic circulation (current flow) with a successive reduction of flow towards the base of the algae, and that higher temperatures are a consequence of internally produced heat (as a product of metabolism and/or decomposition of organic matter or in shallow littoral areas of solar heating), as pointed out by Escartin & Aubrey (1995). Evidence from the aquarium experiment illustrates the potential of the decaying macroalgae to accelerate internal eutrophication by releasing nutrients (phosphorus) bound in the sediment and algae back into the water column (Sundby et al. 1992). Nutrient background levels in the laboratory experiment (control treatment) were high, possibly caused by bacterial production in the stagnant (no flow-through) water. As the algae constitute one of the most important factors inducing hypoxia/anoxia above the halocline in the northern Baltic Sea (Norkko & Bonsdorff 1996), the normally oxic conditions in above-halocline sediments could be subject to increasing phosphorus release from the sediment due to algae-induced oxygen deficiency. This could further accelerate eutrophication.

Habitat modifications induced by the algal mat and responses of the zoobenthic community

The physical presence of the algal mat causes considerable habitat modifications for the zoobenthic community. The algal mat has been shown to form a phys-

ical barrier structuring the zoobenthos at the initial phase of recruitment by the filtering of settling larvae (Ólafsson 1988, Bonsdorff 1992, Bonsdorff et al. 1995). Bonsdorff (1992) showed drifting algal mats to filter more than 70% of settling *Macoma balthica* larvae. Gaines & Roughgarden (1985) emphasized the role of larvae as a determinant of zoobenthic community structure; the negative influences of the drift algal mats are further pronounced since adult infauna (i.e. *M. balthica*) are negatively influenced by drifting algal mats (*sensu* Bonsdorff et al. 1995). As shown by Nicholls et al. (1981), low oxygen concentrations in the underlying sediment would favour the algal mat as a habitat for macrofaunal species on the assumption that they have the capability (mobility) of taking advantage of the algae, and for epibenthic species such as mudsnails, this would be especially expected. In the field experiment, the algae were rapidly colonized by mudsnails. It is uncertain, however, to what degree mudsnails from the underlying sediment succeeded in vertical migrations up into the algae. In samples from the sediment under algae, we recorded considerable amounts of decomposing mudsnail shells.

Infaunal species are known to respond to hypoxia by gradually leaving their protected position in the sediment and emerging at the sediment surface (Jørgensen 1980, Rosenberg et al. 1991). As illustrated by Norkko & Bonsdorff (1996), the response to the combinations of hypoxia, hydrogen sulfide and the physical presence of the algal mat induces a more rapid response than mere hypoxia, illustrating the importance of physical cover and possibly toxic exudates from the algae (Johnson & Welsh 1985, Anéer 1987). Everett (1994) argued that the presence of hydrogen sulfide and its toxicity (Theede et al. 1969) is the main factor inducing infaunal escape responses and mortality. Norkko & Bonsdorff (1996) found 70% of the population of adult *Macoma balthica* to have emerged from the sediment after 17 d of algal cover. Perkins & Abbott (1972) reported similar results with bivalves on the sediment surface, possibly avoiding the unfavourable conditions, and waders were reported to forage on unprotected bivalves. Norkko & Bonsdorff (1996) illustrated the subtle effects of predation by epibenthic predators on prey stressed by temporary covers of drifting algal mats (i.e. effects of intermediate disturbance). In this study, the initial increase in biomass under algae is probably a consequence of adult *M. balthica* emerging closer to the sediment surface. This would mean that adult clams were initially too deep in the sediment for effective sampling with the core-sampler used.

In a field survey conducted by Soulsby et al. (1982), opportunistic polychaetes such as *Capitella capitata* were found to be abundant under algal cover clearly

being favoured by the presence of algae, and similar results have also been reported by others (e.g. Thrush 1986, Raffaelli et al. 1991). In our study, oligochaete species fulfill the same functional role without declines in abundance under algal cover (Bonsdorff 1992, this paper). It seems evident that sedentary infauna such as bivalves and tubicolous species may experience high mortality, while mobile species may to some extent benefit from algal cover. To a certain degree, local macrofaunal activity moved from the sediment to the algal mat, and it seems evident that the algal mats may function as an important rafting mechanism for invertebrate species (Gore et al. 1981), as well as a refuge from predation and an enriched trophic resource (Everett 1994) (Table 3). In a recent paper by Vetter (1994), sublittoral accumulations of algae were found to be inhabited by the highest densities of macrofauna ever found. Still, the drifting algae might be regarded as an insecure habitat for macrofaunal species because of the high degree of instability due to movement and degradation.

The zoobenthic community proved to be vulnerable to the exposure of drifting algae with a community breakdown after 16 d of algal cover. Structural differences were already found after 9 d of exposure. At the end of the experiment, the community breakdown was evident in all measured community parameters. When converting data to a larger scale, the effects of the drift algae become more apparent: 1 ha of bare sand (uncovered) sustains 242 million individuals and 1 t of benthic macrofauna, whereas 1 ha with algal cover sustains 31 million individuals and 0.007 t (7 kg). The natural occurrences of drifting algae in the sound were calculated to cover 2 ha, i.e. 1/3 of the total area.

The field experiment proved to be a powerful tool in evaluating the effects of naturally occurring drifting algal mats, as well. All measured parameters were remarkably similar in both the experiment and the natural field situation. Community development under the algal plots showed decreasing Euclidean distances compared to the natural field situation, illustrating the increase in similarity over time (Table 5).

Despite the fact that algae occur during a restricted period during summer, the effects are severe and the reduction in the standing stock of zoobenthos is bound to have repercussions on higher trophic levels. The degradation of standing stock combined with the reduction of available feeding grounds could affect the flounder populations since adult *Macoma balthica* are known to be their major food source (Bonsdorff et al. 1995). Habitat degradation for epibenthic predators is also supported by our observations of dead fish entangled in the algae. The summer of 1994 was characterized by mass occurrences of benthic drift algae, and

it was the first year we saw dead flounders on several occasions in connection with the algae (probably caused by H_2S poisoning).

Short-term recovery after algal stress

Depending on the severity of algal stress, different levels of resources such as space and food are liberated for colonizing species once the drift algal mat is disintegrated or transported away. Patches generated by the decay of algae may offer abundant food resources in the form of bacteria and decaying algal debris to opportunistic colonizers, such as oligochaetes and mudsnails *Hydrobia* sp. The total number of species available for recolonization is low in the northern Baltic Sea, however, and hence the early phases of recovery are primarily governed by season and the occurrence of different life stages of the dominant fauna (Bonsdorff & Blomqvist 1993). Along with available resources, the initial community establishment in this study may be attributed to the short immigration distances (Günther 1992) and to the behavioural aspects of the immigrating species (Zajac & Whitlatch 1982, Bonsdorff 1989). Despite rapid initial recovery, a considerable amount of time is required for the zoobenthic community to recover to pre-stressed conditions (Bonsdorff & Österman 1985), and as pointed out by Bonsdorff & Blomqvist (1993), community succession in the northern Baltic Sea largely follows the general pattern described for fully marine ecosystems by Pearson & Rosenberg (1978). With increasing spatial and temporal scales of disturbance induced by drifting algal mats, the limited mobility of key species such as *Macoma balthica* will restrict the recolonization potential of the community. The absence of large benthic filter-feeders will therefore also alter local energy transfer in shallow coastal areas (Rosenberg & Loo 1988, Peterson et al. 1994). With larger disturbed areas, it is likely that community succession will be determined by the available pool of larvae and pelagic settling. Since the peak settling and recruitment of many invertebrate species is synchronous with the occurrence of algae, however, community establishment might be unsuccessful.

Concluding remarks

Increasing amounts of drifting algae pose a significant threat to the coastal areas of the northern Baltic Sea. The phenomenon of drifting algae occurs in eutrophic coastal areas around the world. In contrast to algal mats in the intertidal, large amounts of detached algae may be present without being noticed in subtidal

areas. Our study documents a severe deterioration of the zoobenthic community exposed to such algae in a Baltic coastal area. The deeper parts of the Baltic Sea have long been impoverished due to periodic or long-term hypoxia below the halocline, whereas the coastal areas above the halocline have been productive and important in maintaining biodiversity. These important shallow coastal areas are now seriously threatened by the occurrences of drifting algal mats.

Acknowledgements. We thank the Husö biological station for providing excellent working facilities. The Academy of Finland, Swedish Cultural Foundation and the Foundation of Åbo Akademi University are acknowledged for financial support. We are grateful to staff and students at Husö for help with diving and field work. Dr Lisbeth Mathiesen from Aarhus University kindly helped in identifying the algae.

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This article was presented by J. Gray (Senior Editorial Advisor), Oslo, Norway

Manuscript first received: May 5, 1995

Revised version accepted: August 4, 1995